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Long-term affective and non-affective brain alterations across three generations following the genocide in Cambodia

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A R T I C L E I N F O

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A B S T R A C T

The literature has largely indicated that trauma can lead to post-traumatic stress disorder (PTSD) and alterations in brain functioning. However, to what extent these alterations remain present decades after the traumatic event, and how the next generations may also suffer from them, remains unclear, especially in a non-Western culture. Uniquely, the present project focused on survivors of the Cambodian genocide and the subsequent two generations to determine whether brain alterations are observable approximately five decades after the traumatic event and in subsequent generations from the same society. Using portable electroencephalography (EEG), we used four experimental tasks—two targeting non-affective processing (i.e., sensory gating, oddball) and two targeting affective processing (i.e., emotion recognition, threat processing). Results indicated that although the rate of PTSD symptoms was similar across generations, the affective reaction to threat for the LPP and FMθ was primarily observed or intensified in the directly affected generation (i.e., G0), regardless of the presence of PTSD. We also observed that G0 exhibited reduced attenuation over standard tones in the oddball task for the N100 and a reduced sensory gating effect on the auditory P200. The present study underscores that affective and non-affective alterations might still be present decades after a trauma, but are not necessarily observable in subsequent generations. Our results also support a dissociation between reported PTSD symptoms and neural alterations.

1. Introduction

Experiencing trauma can lead to post-traumatic stress disorder (PTSD) and negatively impact various brain functions in early automatic and late conscious processing in both affective and non-affective contexts (Miller et al., 2021). For example, trauma can lead to an increased fear response due to an overactive limbic system (Morey & Brown, 2012), difficulty regulating memories due to an alteration of the hippocampal function (Woon et al., 2010), and a deficit in emotion regulation and attentional bias towards threatening stimuli due to a deficit in prefrontal cortical inhibition of the amygdala (Matsuo et al., 2003). It can also lead to a deficit in information processing, including (pre-)attentive processing of unexpected stimuli (Ge et al., 2011; Kimble et al., 2000; Morgan & Grillon, 1999), encoding new stimuli (Gjini et al., 2013), or filtering out irrelevant information (Gjini et al., 2013; Javanbakht et al., 2011). Importantly, several studies have shown that untreated traumatic experiences have long-lasting impacts on mental health (Marmar et al., 2015) and affect subsequent generations (Yehuda & Lehrner, 2018).

However, despite several meta-analyses and systematic reviews, several gaps in the literature still involve critical unanswered questions, which will be tackled in the present research. Firstly, while a previous study showed that PTSD can manifest even 40 years after a traumatic event (Marmar et al., 2015), it is still unknown whether affective and non-affective neural alterations persist over such extended periods, with or without ongoing PTSD. Second, the existing literature suffers from a WEIRD (Western, Educated, Industrialized, Rich and Democratic) centrism, preventing generalization across different cultural and ethnic populations (Arnett, 2008; Caspar, 2024; Henrich et al., 2010). Cultural neuroscience research has indicated that cultural differences in self-representation modulate many of the same neural processes proposed to be aberrant in PTSD (Liddell & Jobson, 2016), but such work is still very limited, even nonexistant in several regions of the world. Third, even though the literature has evidenced that offspring of traumatized

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parents, with or without PTSD, are more susceptible to developing symptoms of PTSD themselves (Lev–Wiesel, 2007; Roth et al., 2014), it is less clear if neural alterations can also be observed across generations. The literature has shown that several forms of transmission can account for the increased prevalence of PTSD in subsequent generations, whether they are from the same families or not. Several studies have indicated that parental trauma correlates with poorer life outcomes in offspring (Lang & Gartstein, 2018; Van Ee et al., 2016), often manifesting as an increased risk for mental disorders, especially PTSD and depressive symptoms, amongst offspring (Burchert et al., 2017; Goenjian et al., 2008; Wittekind et al., 2017; Yehuda et al., 2008) and altered information processing (Castro-Vale et al., 2020a; Perizzolo et al., 2019; Wittekind et al., 2017; Yehuda et al., 2008). The transmission of trauma across generations can be related to a direct social transmission (e.g., stories heard from family, peers or society (Auerhahn & Laub, 1998)), an indirect social transmission (e.g. parenting practices (Field et al., 2013)), or through genetics (e.g., gene alteration (Perroud et al., 2014)), which explains why both family-related and non-family-related offspring can endure the sequelae of their parents' trauma. Unfortunately, the literature is scarce regarding how affective and non-affective alterations are also present in the following generations, with or without PTSD (Wittekind et al., 2017). A behavioral study showed that both veterans with lifetime PTSD and their offspring have impaired emotion recognition, especially for happiness and disgust (Castro-Vale et al., 2020b). Another study using EEG showed that children of mothers who suffered from maternal interpersonal violence have an attentional bias towards negative emotions in facial stimuli (Perizzolo et al., 2019). EEG findings further indicated that children of those mothers with PTSD had different emotion appraisal and decreased right dorsolateral prefrontal cortex activation in response to angry and fearful faces compared to non-PTSD children. Finally, another study (Wittekind et al., 2017) found that the children of trauma exposed parents presented avoidance tendencies towards parental trauma related stimuli while control children did not present any tendencies. However, these studies only targeted a single potential alteration (e.g., emotion recognition or avoidance tendencies), thus preventing a larger comprehension of the different types of alterations that can be observed in the aftermath of a traumatic event.

To complement the existing literature and bring new elements to the three above-identified gaps (i.e., long-term (non-)affective alterations, underrepresented sample groups, cross-generational transmission), the present study was uniquely conducted in Cambodia with portable electroencephalograms. Under Pol Pot's leadership from 1975 to 1979, the Khmer Rouge regime conducted a brutal social campaign, resulting in a genocide of approximately 1.7–2 million people (~25 %). During that period, the entire Cambodian population suffered, with strong potential effects on subsequent generations (Schaack et al., 2011). We assessed various types of alterations commonly reported in the scientific literature to gain a broader understanding of which alterations may persist in the aftermath of the Cambodian genocide. Among the different tasks commonly used in the literature, we prioritized passive tasks (i.e., 3 out of 4), which only required the visualization of images or listening to sounds. This decision was made because our target population had, in some cases, never interacted with such technology in the past, in order to avoid any interference with our results. We employed four experimental tasks two targeting non-affective processing (i.e., sensory gating; oddball) and two targeting affective processing (i.e., emotion recognition; threat processing). Sensory gating refers to the brain's ability to filter out irrelevant sensory information. In the trauma literature, it has been found that this process may be impaired, leading to heightened sensitivity to environmental stimuli (Schlüter et al., 2019; Schlüter & Bermeitinger, 2017; Sokhadze et al., 2008; Zukerman et al., 2023). The oddball paradigm is a cognitive task used to study attention and event-related potentials by detecting rare or unexpected stimuli. It has been shown that individuals suffering from PTSD often show altered neural responses to such stimuli, indicating disruptions in attentional processing (Han et al., 2018; Veltmeyer et al., 2005). Threat processing is the evaluation and response to potential dangers. In PTSD, this process can be hyperactive, causing exaggerated fear and anxiety responses (DeLaRosa et al., 2020). Finally, emotion recognition involves identifying and interpreting emotional expressions, a process with which individuals with PTSD often struggle, particularly in recognizing and processing negative emotions (Castro-Vale et al., 2020a).

We recruited survivors of the genocide from rural and urban areas in Cambodia, as well as individuals from the first and second generations after the genocide in a cross-generational design, without a direct family link between the generations. To understand if affective and non-affective neural alterations persist even 50 years after a traumatic event, we evaluated the extent to which survivors of the Cambodian genocide (Generation 0) display alterations, depending on the presence or absence of PTSD, as well as in comparison to individuals who did not experience the genocide directly (G1 and G2). Given that no one was spared by the Khmer Rouge regime that lasted about 5 years, it was impossible to find unaffected, matched controls who were also present in the country during that period and still lived there. Since this population had never been approached by neuroscientists before, we lacked clear predictions that would be culturally sensitive enough for our hypotheses. Therefore, our pre-registered hypotheses followed the classic effects observed in the existing literature on Western populations, although our discussion will consider possible cultural differences. If affective and non-affective neural alterations are still present 50 years after trauma, we expected to observe the following: (1) a reduced sensory attenuation on the second stimulus in the sensory gating task for individuals with PTSD compared to those without PTSD, specifically on the P50 (Gjini et al., 2013; Neylan et al., 1999); (2) a higher MMN and P3 in individuals with PTSD compared to those without, indicating increased arousal for unexpected stimuli in the auditory oddball task (Bangel et al., 2017; Felmingham et al., 2002; Ge et al., 2011; Lamprecht et al., 2004; Menning et al., 2008; Morgan & Grillon, 1999); (3) an enhanced LPP and an enhanced mid-frontal theta (FMθ) to threatening or unpleasant images in individuals with PTSD compared to those without PTSD in the threat processing task (Cavanagh & Shackman, 2015; Lobo et al., 2014; Macatee et al., 2021; Sperl et al., 2019); and (4) impairments in recognizing emotions in individuals with PTSD (Miller et al., 2021; Passardi et al., 2018, 2019; Poljac et al., 2011) and the next generation (Castro-Vale et al., 2020b) compared to individuals without PTSD. We also analyzed to what extent such alterations may be observable in G1 and G2, with or without the presence of PTSD. Finally, we performed correlations between the PTSD scores and the neural and behavioral results. The literature is however not fully in agreement, as some papers report those correlations (Araki et al., 2005; Felmingham et al., 2002; Gillette et al., 1997; Gjini et al., 2013; Menning et al., 2008), while others do not (Bangel et al., 2017; Ge et al., 2011). As the main EEG extraction method - based on the peak amplitude or mean amplitude - can account for such differences, we performed both at the exploratory level. Previous literature on PTSD similarly indicates that more correlations emerge with the peak amplitude method (Araki et al., 2005; Felmingham et al., 2002; Gillette et al., 1997; Gjini et al., 2013; Menning et al., 2008) than with the mean amplitude approach (Bangel et al., 2017; Ge et al., 2011).

2. Method

2.1. Participants

The four experiments were pre-registered before data acquisition (Threat: https://osf.io/y4vn3; Emotion Recognition: https://osf.io/qe8vm; Oddball: https://osf.io/ch7dy; Sensory Gating: https://osf.io/fqad6). Power calculations for each experiment indicated that we needed to recruit between N = 96 and N = 126 for a power of 95 % and a medium effect size $f = .25$ (Cohen, 1988), including survivors (Generation 0), the first generation after the genocide (G1) and the second generation (G2), in relation to our within-subject factors and their interactions in each task (see preregistrations). We used a standard medium effect size *f* because no prior studies have approached our target populations with the present experimental design, and because a recent systematic meta-analysis showed that the literature is plagued by insufficient sample sizes in commonly tasks used (Miller et al., 2021). This method to justify sample size is described in (Lakens, 2022). To prevent data loss, we recruited 163 participants (G0 =59; G1 =52 and G2 =52). As indicated in the pre-registrations, individuals were not systematically from the same families. Sixteen individuals had grandparent-grandchild relationships and two individuals had parent-child relationships. This sub-sample was not sufficient to conduct reliable statistical analyses, but we conducted additional exploratory analyses in each task without this sub-sample. Similar to previous studies, a total score > 33 on the Khmer version of the PCL-5 (Schaack et al., 2011) was considered indicative of probable PTSD (Ean et al., 2019). However, the PCL-5 alone is not sufficient to diagnose PTSD and should be complemented by clinical interviews. Thus, when we use the terms PTSD/non-PTSD in the present paper, it should be noted that this is based on the cut-off provided by previous literature, indicative of a probable PTSD diagnosis, not a clinically confirmed PTSD diagnosis. More information regarding the recruitment procedure and the grouping method of participants is presented in Supplementary Information S1. Demographic data are displayed in Table 1. Of note, Generations 1 (G1) and 2 (G2) did not show a marked difference in age, despite a significant age gap and the fact that they belonged to different generations. This is inherent to the circumstances in Cambodia during the Khmer Rouge regime. The regime indeed recruited citizens of all ages, from older adults to teenagers and children, for participation. Consequently, those who lived through the genocide (i.e., G0) exhibit a wide range of ages. This has led to an overlap in the ages of Generations 1 and 2 in the current population. For G0, as part of the Harvard Trauma Questionnaire, we asked whether they had experienced any physical injuries, such as suffocation, drowning, or genocide-related events (see Table 1, Figure S2). These questions were included because many Cambodians experienced severe acts of torture during the genocide and, in some cases, during a brief period of revenge that followed. We did not find a validated questionnaire in Khmer to evaluate the presence of trauma in G1 and G2, so we lacked results for these generations. We simply asked them to indicate verbally if they had experienced any potentially traumatic event that could be traumatic in their lives. No traumatic events were reported based on these verbal reports, beyond some family loss. We followed a strict ethical procedure based on European ethical standards and obtained the approval of the University of Battambang (Figure S1).

2.2. Material & Method

Volunteers were invited to sit in front of a computer screen after signing consent (see Supplementary Information S2). We installed a 32-channel EEG system to record their brain activity and provided them with earplugs to listen to auditory stimuli. After the task, participants filled in the PCL-5 and the Harvard Trauma questionnaire to assess the severity of the trauma (see Supplementary Information S3).

2.2.1. Emotion Recognition

Each trial started with a fixation cross presented for a jittered duration between 1.5 s and 1.8 s (mean: 1.65 s). Volunteers were then presented with 6 Cambodian faces (3 females and 3 males) displaying either a neutral, positive (i.e., happiness) or negative (i.e., sadness) emotion. Below each face, three words (i.e., neutral, happy and sad) written in Khmer were displayed on the screen, together with three emoticons for individuals who could not read (Fig. 1**A**). Volunteers were presented with a 3-button keyboard and were told to press, as fast as possible, the button corresponding to the emotion presented. The picture disappeared after the keypress. As many of the volunteers had never used a keyboard before, we first trained them to press the keys during a training session. Each individual was presented with 48 stimuli, with 16 per emotion. There was thus a total of 288 stimuli used, with 96 per emotion. The task lasted between 7 and 15 minutes.

2.2.2. Threat Processing. Volunteers were invited to passively look at images displayed on the screen. We used two categories of pictures, displaying either humans or animals (Fig. 1**B**). For each category, the pictures displayed a threatening situation from the first-person perspective (i.e., 1PP), from the third-person perspective (i.e., 3PP) or a non-threatening situation (i.e., NoPP). Each trial started with a fixation cross presented for a jittered duration between 1.5 s and 1.8 s (mean: 1.65 s). The pictures were then presented for a fixed duration of 200 ms in a semi-randomized order, such that no two pictures from the same category followed one another. There were 40 trials in each category, thus leading to a total of 240 stimuli. The task duration was about 7.5 minutes.

2.2.3. Sensory Gating. Volunteers were invited to passively look at images displayed on the screen or to listen to tones. Each trial started with a fixation cross presented for a jittered duration between 2.5 s and 3 s (mean: 2.85 s) (Fig. 1**C**). We had three categories of tones: 400 Hz, 800 Hz or 1200 Hz (duration: 200 ms), and three categories of images: triangle, square or round (duration: 200 ms). Tones and images were always presented in pairs, where the first stimulus (S1) was always identical to the second stimulus (S2), with a fixed 500-ms interval between them. Pairs of tones and pairs of images were presented in two different, and counterbalanced experimental blocks. The pairs were presented in a semi-randomized order, such that no two pairs of pictures or tones from the same category followed one another. There were 24 pairs for each category, thus resulting in a total of 144 pairs. The total

Table 1
Demographical and trauma-related information of the recruited sample. Statistical comparisons were two-tailed.

	G0 – N = 59	G1 – N = 52	G2 – N = 52	Group comparisons
Age	66.08 (SD=7.68)	25.55 (SD=8.72)	19.48 (SD=3.71)	G0 > G1 > G2 (all *ps* < .001)
Female/male	34/59 (57.62 %)	39/52 (75 %)	37/52 (71.15 %)	$p > .1$ ($\chi 2$)
PCL−5 score > 33	19/58 (32.75 %)	24/52 (46.15 %)	22/52 (42.30 %)	$p > .2$ ($\chi 2$)
Re-experiencing	7.102 (SD=4.71)	8.606 (SD=5.31)	6.961 (SD=4.96)	$p > .1$
Avoidance	3.271 (SD=2.39)	3.596 (SD=2.36)	2.588 (SD=1.91)	$p > .068$
Negative Alteration	7.458 (SD=5.06)	9.769 (SD=6.60)	9.490 (SD=5.85)	$p > .09$
Hyperarousal	8.937 (SD=4.83)	8.838 (SD=5.80)	8.922 (SD=5.53)	$p > .9$
Previous access to mental health	0/59 (0 %)	0/52 (0 %)	0/51 (0 %)	
Time since traumatic event	48 years	NA	NA	
Years of education	< 6	5–11	5–13	
Ethnicity	59/59 Khmers	52/52 Khmers	52/52 Khmers	
Drowning	2/59 (1 between 75 and 79)	/	/	
Brain injury	10/59	/	/	
Suffocation	20/59 (1 between 75 and 79)	/	/	
Loss of consciousness	12/59 (1 between 75 and 79)	/	/	
Medication during the testing	5/59	/	/	

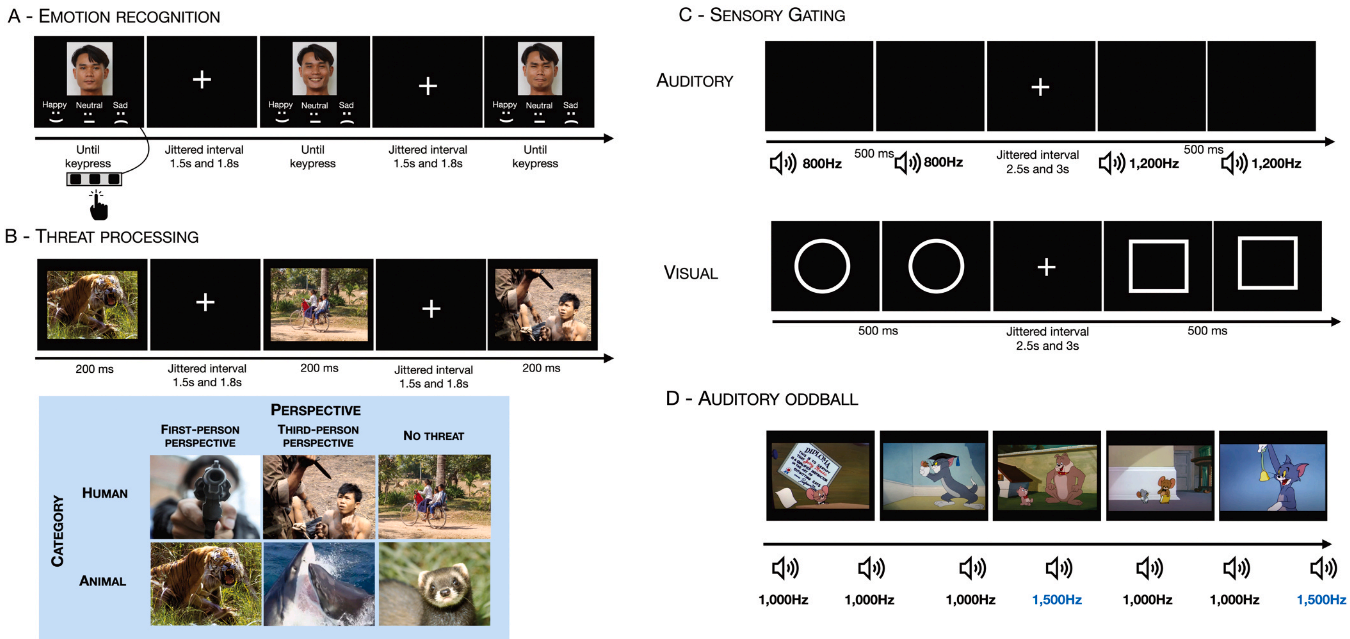

Fig. 1. Figure captions represent the four experimental tasks utilized. A) The emotion recognition task required participants to identify emotions displayed on various faces, which were randomly presented during the task. Note that the figure only displays a single individual's face for illustration. B) The threat processing task involved passive viewing of pictures of humans and animals, depicting threat from the first-person perspective (1PP), third-person perspective (3PP), or without threat (NoPP). C) The sensory gating task required participants to passively observe or listen to two identical stimuli presented with a 500-ms interval. D) The auditory oddball task entailed watching a silent cartoon while being exposed to standard and deviant tones.

task duration was about 8.05 minutes.

2.2.4. Oddball. Volunteers were invited to look at a silent cartoon for 6 minutes (Fig. 1**D**). As many volunteers could not read, there were no subtitles. During those 6 minutes, tones were presented, with 20 % being deviant tones (i.e.,1500 Hz) and 80 % being standard tones (i.e., 1000 Hz). Each tone was presented for a fixed duration of 200 ms. There was a jittered interval between each tone that lasted between 800 ms and 1,2 s (mean: 1 s). No two deviant tones followed one another.

3. Results

General Statistical approach. In the pre-registrations, we initially planned to conduct repeated-measures ANOVA, but we opted for linear mixed models to account for participant variability in the results (Boisgontier & Cheval, 2016). All data, analysis codes, and research materials are available on Open Science Framework (https://osf.io/x6hrn/). Data were analyzed using R. For the MMN in the Oddball task, we kept the planned repeated-measures approach since it involves a subtraction from standard to deviant tones, which cannot be done on a trial basis, given that such tasks involved an unequal number of trials between deviant and standard tones.

In the present study, there was an evident confound between Generation and Age, as individuals in G0 were older than those in G1, who were, in turn, older than those in G2. This issue is inherent in studies investigating cross-generational differences and could undermine the interpretation of a Generation effect, as the observed differences might also be attributed to aging. In Cambodia, finding a control group that had not experienced the genocide was impossible. The Khmer Rouge regime spread its ideology and brutality across the entire country for five years, sparing no one from violence. Recruiting a control group from another country, whether neighboring or not, would have been inappropriate due to significant differences in history, culture, education, social context, and access to mental health infrastructure. As a result, we consistently used 'Age' as a covariate. Any significant interactions involving the 'Generation' factor, but not showing significant interactions with the 'Age' factor, were interpreted as reliable Generation effects. In the first model (Model 1), we z-scored age across participants before including it in the analysis. However, multicollinearity, measured by the Variance Inflation Factor (VIF), was found to be extremely high when both Age and Generation were included in the same model (i.e., all max VIFs > 349; Kim, 2019), thus preventing interpretation of the results (see https://osf.io/x6hrn/ for the VIFs across tasks for this model). We thus centered Age across groups in a second model (Model 2), which led to acceptable VIFs (see also https://osf.io/x6hrn/). However, this method is not perfect, as it only accounts for the effect of Age within each generation and does not mitigate the effect of Age differences between generations. Therefore, we cannot exclude the possibility that the observed effects may be partially explained by overall changes in Age across generations. We also tested a third type of model with 'Gender' as a covariate, but the VIFs were still too high (all max VIFs > 22), which prevented us from running and interpreting this model.

Given the number of experiments (i.e., 4) and analyses conducted in the present study, we primarily focused on interactions that were relevant to our research questions. These included the factors of Generation or PTSD in relation to our manipulated variables, in order to reduce the risk of alpha errors. Post-hoc comparisons were systematically using a False Discovery Rate (FDR) correction to maintain an acceptable alpha risk in the context of multiple testing (Benjamini & Hochberg, 1995; Midway et al., 2020).

Outliers were removed from all tasks, including behavioral and electroencephalographic (EEG) data, using a combination of outlier detection methods. Outliers were defined as values detected as outliers by at least two of the following methods: 2.5 times the Median Absolute Deviation (MAD; Leys et al., 2013, 2019), 1.5 times the Interquartile Range (IQR; Hoaglin et al., 1986; Jones, 2019), and 2.5 times the Standard Deviation (SD; Berger & Kiefer, 2021; Yang et al., 2019). This approach allowed us to benefit from the strengths of each method while reducing biases in the outlier removal procedure.

The plots display Standard Errors corresponding to the within-subject and/or between-subject effects as shown in the graphs.

EEG recording and processing. EEG data were acquired at 2048 Hz from 32 channels placed according the international 10–20 system using ActiveTwo Biosemi equipment (see http://www.biosemi.com for hardware details). Four additional electrodes were used to acquire horizontal eye movement and mastoid signals. All the data were recorded using the the ActiView software.

Event-related potentials. Data were processed using MNE-Python (Gramfort et al., 2013). The data were downsampled to 512 Hz, and a bandpass filter between 0.3 and 40 Hz was applied. We used the default parameters of the filter function from the MNE-python library (https://mne.tools/stable/generated/mne.io.Raw.html#mne.io.Raw.filter). This resulted in a zero-phase Finite Impulse Response (FIR) filter, using a Hamming window. The filter length is 6.6 times the reciprocal of the shortest transition band. The low-cutoff and high-cutoff transition band are calculated based on the lower and higher frequency chosen. Bad channels were identified visually and interpolated (mean = 1.46, SD = 2.38). A duplicate dataset was created to apply an automatic ICA, with the number of components calculated to represent 99.99 % of the data. This dataset was high-pass filtered at 1 Hz. Eye movements (blinks and saccades) were detected using the find_bad_eog function in MNE-Python, which calculates correlations between independent components and EOG-labeled electrodes. EOG detection included horizontal electrodes and the vertical 'Fp1' and 'Fp2' electrodes. Components with correlations above 0.5 were removed from the original data (mean = 2.21, SD = 0.95). The duplicate dataset was not used further. Electrodes for each task were determined based on prior studies (Sensory gating: (Gjini et al., 2013); Auditory oddball: (Ge et al., 2011); Emotion recognition/Threat: (DiGangi et al., 2017)). Epochs and baselines varied across tasks: sensory gating (-200–700 ms, baseline: −50 ms to 50 ms), oddball task (-100–500 ms, baseline: −50 ms to 50 ms), emotion recognition (-100ms to 1500 ms, baseline: −300 ms to −100 ms), and threatening task (-100ms to 1500 ms, baseline: −300 ms to −100 ms). Baseline corrections were applied to longer epochs, which were re-segmented for improved visualization.[1]

ERPs were identified through visual inspection of the grand averages and prior literature (Sensory gating: (Gjini et al., 2013); Auditory oddball: (Ge et al., 2011); Emotion recognition/Threat: (DiGangi et al., 2017)). To align the peaks for the oddball and sensory gating tasks, we shifted the trials based on the averaged most negative peak found for each participant within a time window of 50–250 ms for the oddball task and 100–300 ms for the sensory gating task. This shift ensured that the minimum peak was centered at 150 ms for each participant. Moreover, we observed that, on one of the computers, the peaks were more delayed for participants in the oddball task due to a slight change in the implementation of the triggers. For these participants, we identified the minimum peak within a time window of 350–550 ms. For the threat processing task, N1 was extracted within the 50–170 ms time window, P2 within 148–248 ms, N2 within 235–408 ms, and P3/LPP within 380–1000 ms. For sensory gating in the visual modality, P50 was extracted within the 60–110 ms time window, N1 within 110–175 ms, and P2 within 200–350 ms. For sensory gating in the auditory modality, P50 was extracted within the 45–93 ms time window, N1 within 93–200 ms, and P2 within 200–350 ms. For the auditory oddball task, P50 was extracted within the 40–110 ms time window, N1 within 110–200 ms, and P2 within 200–315 ms. For the emotion recognition task, P3 was extracted within the 250–600 ms time window. For this latter task, we were unable to extract the Late Positive Potential (LPP) concurrently with P3, as participants typically moved their heads while pressing the buttons, causing large head movements around 450 ms after stimulus presentation. Despite instructions to keep their heads still, pressing buttons was an entirely new task for most participants, leading many to check the button-pressing mechanics before taking action. Consequently, only the P3 was analyzed, with only the peak considered to avoid including the negative deflection in data extraction.

We employed a mean-to-mean method to extract the amplitude of each ERP (Heise et al., 2022; Luck, 2005). Peak amplitude values tend to be more biased by noise than mean amplitude values. Moreover, extracting values at the trial level is even more influenced by noise compared to aggregated data typically used in ANOVA methods (Hu et al., 2011; Mir et al., 2014). Therefore, we opted to use the mean amplitude method for our mixed models analysis, accounting for variability at the trial level. Given the notable differences reported in the literature regarding correlations, we also extracted peak-to-peak amplitudes for exploratory correlations, which were compared to the mean-to-mean approach for the same correlations.

Time-frequency representation (TFR) analysis. Following established literature (Cohen and Cavanagh, 2011; Cohen & Donner, 2013), we computed the frontal midline theta frequency (FMθ) by averaging the Fz, Cz, FC1, and FC2 electrodes. Time-frequency power was extracted for each trial using the tfr_morlet() function in MNE-Python. The parameters used included a frequency range of 2 Hz to 30 Hz with 80 logarithmically spaced bins, logarithmically spaced cycles from 4 to 14, and a Fast Fourier Transform. As mentioned earlier, the epochs analyzed ranged from −2.5 s to 2.5 s around the keypress (stimulus-locked). All power values in the TFR were normalized using a full-epoch-length single-trial correction (see further details in Grandchamp & Delorme, 2011). We first performed normalization over the full epoch length within each trial and frequency. The full epoch was defined as −1.5 s to 1.5 s (instead of the −2.5 s to 2.5 s window used earlier) to avoid edge artifacts (Kaiser & Schütz-Bosbach, 2021; van Driel et al., 2012). The mean and standard deviation (SD) of this period were computed for each trial. Each time-frequency point was normalized by subtracting the mean and dividing by the SD of the same trial. Subsequently, we calculated the average and SD of all trials within the baseline window period of −0.5 s to 1.5 s to avoid overlap with the previous trial, given that the fixation cross lasted 500 ms. Each trial was re-normalized using the averaged baseline and divided by its SD baseline. In summary, this method first normalized the full-epoch values, followed by re-normalization using the average baseline across epochs. Epochs were cropped from −0.5 s to 1 s, and averages were computed across all conditions and participants. To identify significantly different values within the time-frequency data, we selected those exceeding the mean + 1.96 * SD of all values. This formula defines a range within which the true population mean is expected to fall with 95 % confidence (i.e., 95 % confidence; Field, 2012). The selected values were used to create a circular mask for extracting FMθ power within specific time and frequency windows. Finally, for each participant, the mean value within this mask defined the time-frequency window.

For all EEG epochs, outliers were removed based on peak-to-peak and mean values using the same method. In the sensory gating task, outliers were calculated for the period from 0 to 400 ms using the average of Fz and Cz electrodes, resulting in 11.94 % outliers (SD = 7.53). In the oddball task, outliers were calculated for the same period, resulting in 10.59 % outliers (SD = 7.63). In the emotion recognition task, outliers were calculated for the period from 300 ms to 700 ms using the average of Cz, Pz, CP1, and CP2 electrodes, resulting in 14.10 % outliers (SD = 10.86). In the threatening task, outliers were calculated for the time-domain analysis across 100–300 ms and 300–1200 ms, resulting in 21.88 % outliers (SD = 11.78). For the time-frequency domain analysis in the threatening task, outliers were calculated for the period from 100 ms to 800 ms using Fz, Cz, FC1, and FC2 electrodes, resulting in 14.09 % outliers (SD = 11.27). Finally, visual inspection was performed to check for remaining artifacts, and any significant artifacts (e.g., sweating, head movements) were removed. The overall percentage of outliers after visual inspection was as follows:

[1] The choice of baseline in the case of peak/mean amplitude extraction must be carefully considered and selected within a period similarly affected by the condition. Here, we chose this baseline for visual purposes, as our analysis is based on mean-to-mean amplitude and is no longer influenced by the choice of baseline.

sensory gating task – 16.74 % (SD = 9.17); oddball task – 13.25 % (SD = 12.79); emotion recognition task – 13.25 % (SD = 12.79); threatening task (time-domain) – 22.22 % (SD = 13.50); threatening task (time-frequency domain) – 14.09 % (SD = 11.27).

3.1. Emotion Recognition

For correct responses, we conducted a GLMM with a binomial distribution with Condition (happy, sad, neutral) as a within-subject factor, and PTSD (yes, no) and Generation (G0, G1, G2) as between-subject factors. Participants were included as a random grouping factor with a random intercept and a random slope for Condition. The fixed effects included Condition, PTSD, Generation, centered Age, and their interaction (correct responses ∼ Condition * Generation * centered Age * PTSD + (Condition | Participant)). The model initially failed to converge using the default optimizer, but convergence was achieved using the BOBYQA optimizer with increased maximum iterations (maxfun = 1^{e6}). We observed a main effect of Generation (χ^2=11.656, p = .002), see Fig. 2**A**. Post-hoc comparisons indicated that G0 had a lower chance of having a correct response (mean: 0.75, CI_{95}:[0.66,0.82]) than G1 (mean: 0.85, CI_{95}:[0.80,0.90]; OR:0.503, CI_{95}:[0.26, 0.99], z ratio: −2.437, p_{FDR} =.022), and than G2 (mean: 0.88, CI_{95}:[0.84,0.92]; OR:0.387, CI_{95}:[0.19, 0.77], z ratio: −3.314, p_{FDR} =.002). G1 and G2 did not differ (p > .3). We also observed a main effect of Condition (χ^2=218.183, p < .001). Post-hoc comparisons indicated that the probability of correct responses was higher for happy faces (mean: 0.97, CI_{95}:[0.96,0.98]) than neutral faces (mean: 0.71, CI_{95}:[0.65,0.76]; OR:14.08, CI_{95}:[8.79, 22.56], z ratio: 13.438, p_{FDR} <.001), and than sad faces (mean: 0.61, CI_{95}:[0.57,0.66]; OR:21.71, CI_{95}:[12.74, 36.98], z ratio: 13.832, p_{FDR} <.001). The probability for correct responses was also higher for neutral faces compared to sad faces (OR:1.54, CI_{95}:[1.04, 2.27], z ratio: 2.664, p_{FDR} =.007). All the other significant interaction involved centered Age and were not investigated further. All the other main effect or interactions were not significant (all ps > .09).

The same LMM was conducted excluding individuals with family links. The main effect of generation became non-significant (p > .1). We also observed an interaction Generation*PTSD (χ^2=6.979, p = .030). Post-hoc comparisons indicated that for individuals without PTSD, Generation 0 (mean: 0.74, CI_{95}:[0.65,0.82])) had a lower probability of having a correct response than G1 (mean: 0.89, CI_{95}:[0.83,0.93]); OR:0.339, CI_{95}:[0.12, 0.93], z ratio: −3.149, p_{FDR} =.012) and G2 (mean: 0.91, CI_{95}:[0.85,0.94]); OR:0.292, CI_{95}:[0.10, 0.29], z ratio: −3.467, p_{FDR} =.007). G1 and G2 did not differ (p_{FDR} >.1). When comparing individuals with PTSD, all differences across generations were non-significant (all ps_{FDR} >.6). Across generations, the differences between individuals with PTSD and individuals without PTSD were also not significant (all ps_{FDR} >.1). All the other significant interaction involved centered Age and were not investigated further. All the other main effect or interactions were non-significant (all ps > .1).

For response times (RTs), we conducted a LMM with Condition (happy, sad, neutral) and correct responses (correct, incorrect) as within-subject factors, and PTSD (yes, no) and Generation (G0, G1, G2) as between-subject factors. Participants were included as a random grouping factor with a random intercept and a random slope for Condition. The fixed effects included Condition, PTSD, Generation, centered Age, and their interaction (RTs ∼ Condition * Generation * Correct response * centered Age * PTSD + (Condition | Participant)). We observed a main effect of Generation (χ^2=14.455, p < .001). Post-hoc comparisons indicated that G0 (mean: 3.06, CI_{95}:[2.50,3.61]) was slower than G1 (mean: 1.92, CI_{95}:[1.39,2.46]; $mean_{diff}$ = 1.132, CI_{95}:[0.21,2.05], z ratio: 2.890, p_{FDR} =.005) and G2 (mean: 1.63, CI_{95}:[1.09,2.17]; $mean_{diff}$ = 1.427, CI_{95}:[0.50,2.35], z ratio: 3.608, p_{FDR} <.001). We also observed a main effect of correct responses (χ^2=5.482, p = .019), with faster RTs for correct responses (mean: 2.02, CI_{95}:[1.77,2.28]), than for incorrect responses (mean: 2.38, CI_{95}:[1.96,2.80], $mean_{diff}$ = 0.357, CI_{95}:[0.06,0.66]). Other interactions or main effects were non-significant (all ps > .065).

The same LMM was conducted excluding individuals with family links. The pattern of results remained similar, with again a significant main effect of Generation only (χ^2=9.143, p = .01).

For the P300 (see Fig. 2**B**), we observed a main effect of Generation (χ^2=87.256, $p \leq$ .001). Post-hoc comparisons indicated that the amplitude of the P300 was higher for G0 (mean: 10.19, CI_{95}:[9.03,11.35]) than for G1 (mean: 4.51, CI_{95}:[3.40,5.62]; $mean_{diff}$ = 5.68, CI_{95} = [3.72, 7.64], z ratio: 6.941, p_{FDR} <.001) and G2 (mean: 2.88, CI_{95}:[1.77,3.98]; $mean_{diff}$ = 7.32, CI_{95} = [5.36, 9.27], z ratio: 8.958, p_{FDR} <.001). The difference between G1 and G2 was also significant, with a greater amplitude of the P300 for G1 compared to G2 ($mean_{diff}$ = 1.64, CI_{95} = [-0.27, 3.55], z ratio: 2.048, p_{FDR} =.040). All other main effects or interactions were non-significant (all ps > .1).

The same LMM was conducted excluding individuals with family links. We observed a novel interaction Generation*PTSD (χ^2= 6.832,

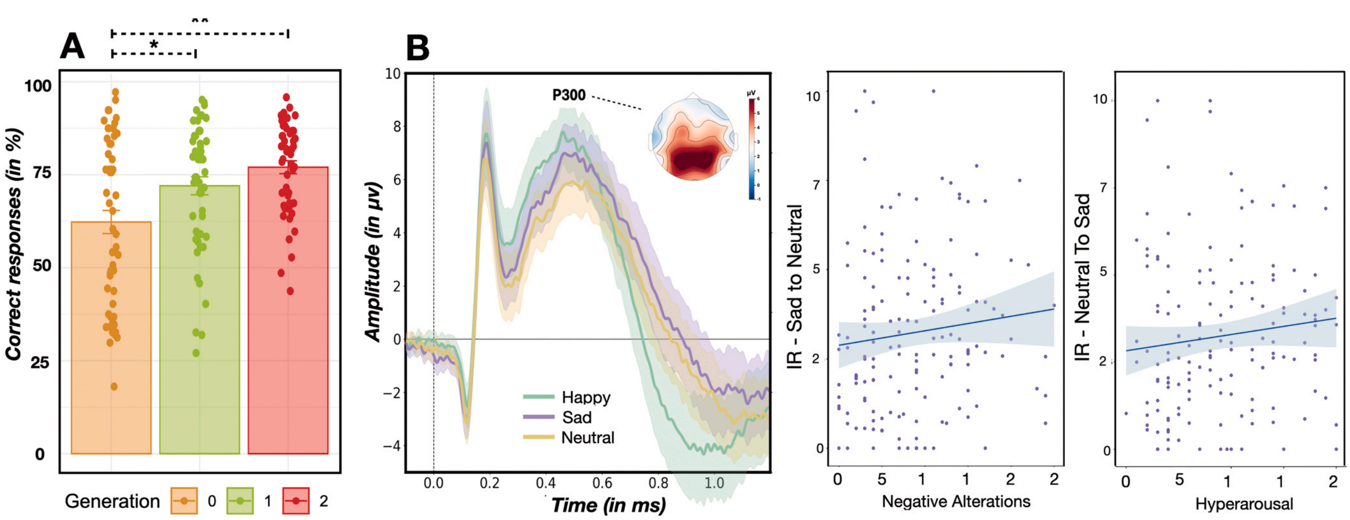

Fig. 2. A) Graphical representation of the percentage of correct responses across G0 (orange), G1 (green) and G2 (red). Dots represent individual data points. All tests were two-tailed. * * represents $p \leq .01$ & $> .001$. * represents a $p > .01$. Error bars represent the Standard Error. B) Grand averaged waves on Cz and Pz from all participants for happy (light green), sad (light violet) and neutral (yellow) faces. C) Graphical representation of the correlations between incorrect categorizations of sad faces as neutral faces and the Negative alteration subscale (left plot), and of the correlations between incorrect categorizations of neutral faces as sad faces and the Hyperarousal subscale (right plot). All tests were two-tailed.

$p = .032$), which was not significant before ($p > .2$). Within generations, no significant differences were observed between individuals with PTSD and those without PTSD (all $ps_{FDR} > .1$). When comparing individuals with PTSD across generations, we observed that G0 had a higher amplitude of the P3 (mean: 7.95, CI_{95}:[5.61,10.28]) than G2 (mean: 4.16, CI_{95}:[3.33,6.66]; $mean_{diff} = 3.782$, CI_{95} = [-0.53, 8.09], z ratio: 2.573, $p_{FDR} = .02$). G1 and G2, and G0 and G1 did not differ (all $ps_{FDR} > .070$). When comparing individuals without PTSD across generations, we observed that G0 had a higher amplitude of the P3 (mean: 10.36, CI_{95}:[9.09,11.63]) than G1 (mean: 3.84, CI_{95}:[2.37,5.30]; $mean_{diff} = 6.524$, CI_{95} = [3.62, 9.43], z ratio: 6.592, $p_{FDR} < .001$) and G2 (mean: 4.16, CI_{95}:[3.33,6.66]; $mean_{diff} = 8.323$, CI_{95} = [5.25, 11.39], z ratio: 7.953, $p_{FDR} < .001$). G1 and G2 did not differ (all $ps_{FDR} > .1$).

Correlations. We performed exploratory Pearson correlations between the PCL-5 subscales (i.e., re-experiencing, avoidance, negative alterations, hyperarousal), the HTQ questionnaire (for G0 only) and the behavioral miscategorisations. Overall, we observed that a higher number of incorrect categorizations of neutral faces to sad faces was associated with a higher score on the hyperarousal subscale (r = .199, p_{FDR}=.050, Fig. 2C), and a higher number of incorrect categorizations of sad faces to neutral faces was associated with a higher score on the negative alteration subscale (r = .180, p_{FDR}=.050). We then performed similar correlations on RTs when correctly identifying happy, sad and neutral faces. We observed a marginal negative correlation between the scores on the negative alteration subscale and RTs for sad faces (r = -.218, p_{FDR}=.052). We also observed a negative correlation between the scores on the negative alteration subscale and RTs for incorrect categorizations of neutral faces as sad faces (r = -.287, p_{FDR}=.036). Other correlations were non-significant (all $ps_{FDR} > .1$).

For the P3, we performed similar correlations but none of them were significant (all $ps_{FDR} > .2$).

3.2. Threat Processing

We conducted LMM with Category (animal, human) and Perspective (1PP, 3PP, NoPP) as within-subject factors, and PTSD (yes, no) and Generation (G0, G1, G2) as between-subject factors on the stimulus-locked LPP (see Fig. 3A) and FMθ (see Fig. 4A with the extraction mask). Participants were included as a random grouping factor with a random intercept and a random slope for Category and Perspective. The fixed effects included Category, Perspective, PTSD, Generation, centered Age, and their interaction (ERP ~ Category * Perspective * Generation * PTSD * centered Age + (Category + Perspective | Participant)).

For the LPP, we observed a significant main effect of Generation (χ^2=23.540, $p < .001$), a significant interaction Generation*Category (χ^2=6.307, $p = .042$) and a significant triple interaction Generation*Category*Perspective (χ^2=10.691, $p = .030$), see Fig. 3B. The interaction Age centered*Category*Perspective was not significant ($p > .088$), suggesting that Generation better explained the effects than age. We thus conducted post-hoc comparisons to analyze the triple interaction Generation*Category*Perspective. The only comparison that survived the correction for multiple comparisons when comparing each perspective within each generation was for the G0, with a higher LPP for the 1PP in the human category (mean: 12.08, CI_{95}:[10.54,13.62]) compared to the NoPP (mean: 9.79, CI_{95}:[8.22,11.36], $mean_{diff}$ = −2.293, CI_{95}:[-4.07, −0.51], z ratio: −3.858, $p_{FDR} = .002$). All other comparisons were non-significant (all $ps_{FDR} > .1$).

We then compared the effect of Perspective on the LPP for each category across generations. We observed that for the 1PP in the human category, G0 had a higher LPP compared to both G1 (mean: 7.5, CI_{95}:[6.06,9.09]; $mean_{diff} = 4.06$, CI_{95}:[0.69,7.42], z ratio: 3.612, $p_{FDR} = .001$) and G2 (mean: 5.71, CI_{95}:[4.12,7.29]; $mean_{diff} = 6.61$, CI_{95}:[3.19,10.04], z ratio: 5.776, $p_{FDR} < .001$). G1 and G2 did not differ ($p_{FDR} > .2$). The effect was similar for the 3PP, with G0 having a higher LPP (mean: 10.86, CI_{95}:[9.42,12.30]) compared to both G1 (mean: 6.94, CI_{95}:[5.51,8.36]; $mean_{diff} = 3.41$, CI_{95} = [0.28,6.54], z ratio: 3.264, $p_{FDR} = .002$) and G2 (mean: 6.09, CI_{95}:[4.60,7.59]; $mean_{diff} = 4.56$, CI_{95} = [1.23,7.89], z ratio: 4.094, $p_{FDR} < .001$). G1 and G2 did not differ ($p_{FDR} > .2$). For the NoPP, G0 had a higher amplitude of the LPP (mean: 9.79, CI_{95}:[8.22,11.36]) than G2 (mean: 5.47, CI_{95}:[3.84,7.10]; $mean_{diff}$ = 3.89, CI_{95} = [0.39,7.39], z ratio: 3.3252, $p_{FDR} = .002$). The difference between G0 and G1, and G1 and G2, were not significant (all $ps_{FDR} > .1$). In the animal category, the pattern of results was similar. For the 1PP, G0 had a higher LPP (mean: 9.53, CI_{95}:[7.94, 11.13]) compared to G2 (mean: 6.31, CI_{95}:[4.66, 7.95]; meandiff = 4.06, CI_{95}:[0.58, 7.55], z ratio = 3.490, $p_{FDR} = .001$), and G1 (mean: 8.02, CI_{95}:[6.45, 9.60]) had a

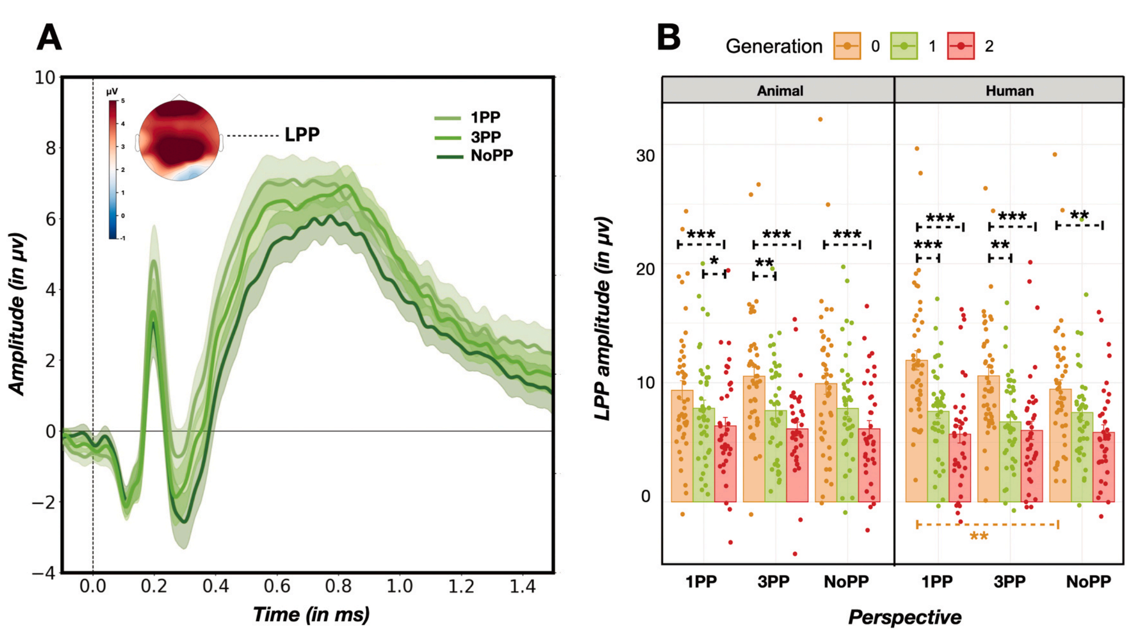

Fig. 3. A) Grand averaged waves on Pz, Cz and Fz from all participants for the first-person perspective (1PP, lighter green), for the third-person perspective (3PP, medium green), and for the no threat (NoPP, darker green). B) Graphical representation of LPP amplitude for each perspective in the animal (on the right) and in the human (on the left) categories across G0 (orange), G1 (green) and G2 (red). Dots represent individual data points. All tests were two-tailed. * ** represents $p \leq .001$; * * represents $p \leq .01$ & $> .001$. Error bars represent the Standard Error.

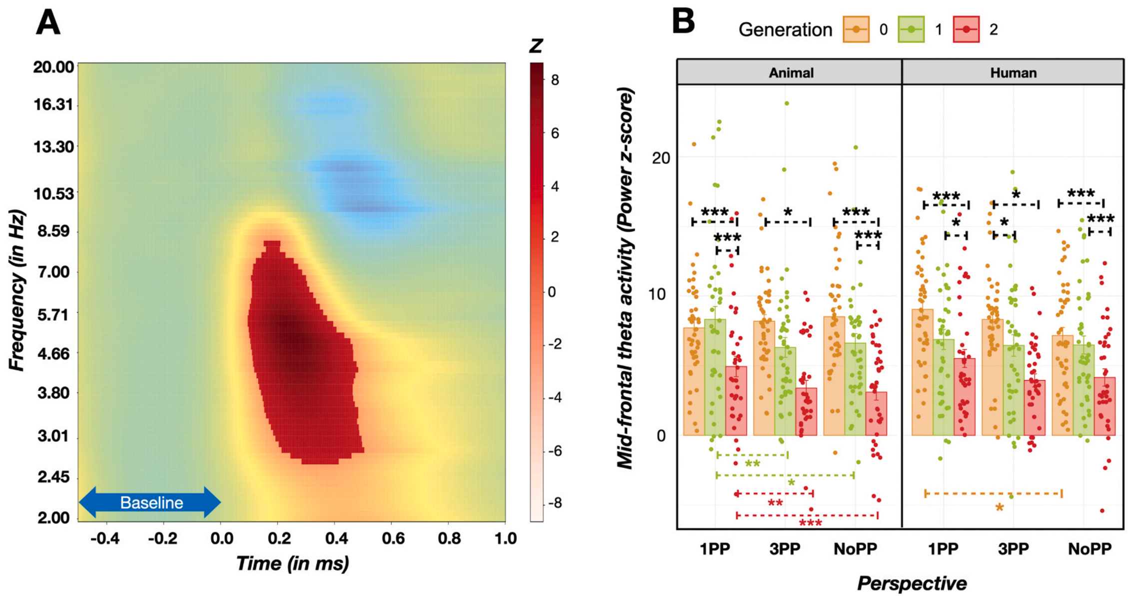

Fig. 4. A) The Time Frequency Representation (TFR) by averaging across all participants and conditions in the threatening task. Specifically, we extracted the average (FMθ) within the mask (dark red) for each participant and condition using Fz, Cz, FC1, and FC2 electrodes. B) Graphical representation of FMθ for each perspective in the animal (on the right) and in the human (on the left) categories across G0 (orange), G1 (green) and G2 (red). Dots represent individual data points. All tests were two-tailed. * ** represents $p \leq .001$; * * represents $p \leq .01$ & $> .001$. * represents a $p > .01$. Error bars represent the Standard Error.

higher amplitude than G2 (2.56, CI_{95}:[-0.90, 6.02], z ratio = 2.208, p_{FDR} =.049). G0 and G1 did not differ (p_{FDR} >.2). For the 3PP, G0 also had a higher LPP (mean: 10.97, CI_{95}:[9.50, 12.45]) compared to both G1 (mean: 7.45, CI_{95}:[5.99, 8.91]; meandiff = 3.52, CI_{95}:[0.36, 6.69], z ratio = 3.229, p_{FDR} =.002) and G2 (mean: 6.16, CI_{95}:[4.62, 7.69]; meandiff = 4.67, CI_{95}: [1.30, 8.03], z ratio = 4.145, p_{FDR} <.001). G1 and G2 did not differ (p_{FDR} >.2). For the NoPP, G0 had a higher amplitude of the LPP (mean: 10.25, CI_{95}:[8.64, 11.86]) than G2 (mean: 5.90, CI95: [4.23, 7.57]; meandiff = 4.35, CI_{95}:[0.81, 7.90], z ratio = 3.678, p_{FDR} =.001). The difference between G0 and G1, and G1 and G2, were not significant (all ps_{FDR} >.086). There was a quadruple interaction Generation*Perpective*Category*centered Age that was significant (p = .02) but not investigated further as not directly relevant for our main hypotheses and as having a VIF > 20. Other interactions or main effects were not significant (all ps > .059).

The same LMM was conducted excluding individuals with family links. A triple interaction Category*Perspective*PTSD appeared (χ^2=7.589, p = .022), though it was marginal in the model with all participants (p = .061). Post-hoc comparisons revealed no significant differences between PTSD and No PTSD individuals (all ps_{FDR} >.3). Similarly, comparisons across perspectives and categories for individuals with PTSD or those without PTSD were not significant (all ps_{FDR} >.3). Other comparisons were not relevant to our research questions and were not further investigated.

For FMθ, we observed a main effect of Perspective (χ^2=24.764, p < .001), with a greater FMθ for 1PP (mean: 7.03, CI_{95}:[6.27,7.78]) than from 3PP (mean: 6.01, CI_{95}:[5.33,6.69], $mean_{diff}$ = 1.017, CI_{95} = [0.44, 1.59], z ratio: 4.133, p_{FDR} ≤.001) and than from NoPP (mean: 5.92, CI_{95}:[5.22,6.61], $mean_{diff}$ = −1.118, CI_{95} = [-1.70, −0.52], z ratio: −4.510, p_{FDR} ≤.001). The difference between 3PP and NoPP was not significant (p_{FDR} >.6). We also observed an interaction Category*Perspective*Generation (χ^2=13.297, p = .009), see Fig. 4**B.** The interaction centered Age*Category*Perspective was not significant (p > .3), suggesting that Generation better explained the effects than age. We thus conducted post-hoc comparisons to analyze the triple interaction Generation*Category*Perspective. Post-hoc comparisons indicated that for G0 in the animal category, there was no effect of Perspective (all ps_{FDR} >.4). In the human category for G0, the FMθ was higher for the 1PP (mean: 8.99, CI_{95}:[7.61, 10.37]) compared to the NoPP (mean: 7.26, CI_{95}:[5.96, 8.56], $mean_{diff}$ = −1.726, CI_{95} = [-3.47, 0.015], z ratio: −2.966, p_{FDR} =.013). Other comparisons were not significant (all ps_{FDR} >.2). For G1 and G2, the effects were reversed as the effect of Perspective appeared in the animal category but not in the human category. For G1 and G2, all comparisons in the human category were indeed not significant (all ps_{FDR} >.063). In the animal category in G1, the FMθ was higher for 1PP (mean: 7.96, CI_{95}:[6.52, 9.40]) than for 3PP (mean: 6.08, CI_{95}:[4.75,7.42], $mean_{diff}$ = 1.882, CI_{95} = [0.17, 3.59], z ratio: 3.294, p_{FDR} =.006) and NoPP (mean: 6.54, CI_{95}: [5.19,7.88], $mean_{diff}$ = −1.426, CI_{95} = [-3.14, 0.28], z ratio: −2.493, p_{FDR} =.045). The 3PP and the NoPP did not differ (p_{FDR} >.5). In the animal category for G2, the pattern was similar, with a higher FMθ for 1PP (mean: 5.48, CI_{95}:[3.97, 6.99]) than for 3PP (mean: 3.45, CI_{95}: [2.05,4.85], $mean_{diff}$ = 2.032, CI_{95} = [0.24,3.82], z ratio: 3.397, p_{FDR} =.006) and NoPP (mean: 3.08, CI_{95}:[1.68,4.49], $mean_{diff}$ = −2.397, CI_{95} = [-4.19,-0.60], z ratio: −3.997, p_{FDR} =.001). The 3PP and the NoPP did not differ (p_{FDR} >.6). There were also some interactions that were significant with centered Age, but these interactions were not investigated further as not relevant for our research questions and having high VIFs > 10. Other interactions or main effects were non-significant (all ps > .070).

We then compared the effect of Perspective on the FMθ for each category across generations. For the 1PP in the human category, G0 had a higher FMθ (mean: 8.99, CI_{95}: [7.61, 10.37]) compared to G2 (mean: 5.45, CI_{95}: [4.02, 6.87]; $mean_{diff}$ = 4.912, CI_{95}: [1.97, 7.85], z ratio: 5.003, p_{FDR} <.001), and G1 had a higher amplitude compared to G2 (mean: 6.71, CI_{95}: [5.36, 8.07]; $mean_{diff}$ = 2.210, CI_{95}: [0.48, 6.42], z ratio: 2.338, p_{FDR} =.034). G0 and G1 did not differ significantly (p_{FDR} >.3). For the 3PP, G0 had a higher FMθ (mean: 8.18, CI_{95}: [6.94, 9.42]) compared to G2 (mean: 4.10, CI_{95}: [2.82, 5.38]; $mean_{diff}$ = 2.698, CI_{95}: [-0.289, 5.68], z ratio: 2.702, p_{FDR} =.015), and compared to G1 (mean: 6.20, CI_{95}: [4.97, 7.42]; $mean_{diff}$ = 2.099, CI_{95}: [-0.68, 4.88], z ratio: 2.255, p_{FDR} =.039). The difference between G1 and G2 was not significant (p_{FDR} >.2). For the NoPP, G0 had a higher FMθ (mean: 7.26, CI_{95}: [5.96, 8.56]) than G2 (mean: 4.07, CI_{95}: [2.73, 5.42]; $mean_{diff}$ = 4.176, CI_{95}:[1.25, 7.10], z ratio: 4.274, p_{FDR} <.001), and G1 had a higher FMθ than G2 ($mean_{diff}$ = 3.452, CI_{95}: [0.48, 6.42], z ratio: 3.481, p_{FDR} =.001). G0 and G1 did not differ significantly (p_{FDR} >.4). In the animal category, the pattern of results was overall similar. For the 1PP, G0 had a higher

FMθ (mean: 7.58, CI_{95}: [6.11, 9.05]) compared to G2 (mean: 5.48, CI_{95}: [3.97, 6.99]; $mean_{diff}$ = 3.504, CI_{95}: [0.47, 6.54], z ratio = 3.455, p_{FDR} =.001), and G1 (mean: 7.96, CI_{95}: [6.52, 9.40]) had a higher amplitude than G2 (mean difference = 3.888, CI_{95}: [0.88, 6.89], z ratio = 3.870, p_{FDR} <.001). G0 and G1 did not differ significantly (p_{FDR} >.7). For the 3PP, G0 had a higher FMθ (mean: 8.06, CI_{95}: [6.71, 9.42]) compared to G2 (mean: 3.45, CI_{95}: [2.05, 4.85]; $mean_{diff}$ = 2.582, CI_{95}: [-0.52, 5.68], z ratio = 2.493, p_{FDR} =.025), but the difference between G0 and G1 (p_{FDR} >.06) and between G1 and G2 (p_{FDR} >.2) was not significant. For the NoPP, G0 had a higher FMθ (mean: 8.26, CI_{95}: [6.90, 9.62]) than G2 (mean: 3.08, CI_{95}: [1.68, 4.49]; $mean_{diff}$ = 5.174, CI_{95}: [2.17, 8.16], z ratio: 5.179, p_{FDR} <.001), and G1 had a higher FMθ (mean: 6.54, CI_{95}: [5.19, 7.88]) than G2 ($mean_{diff}$ = 3.452, CI_{95}: [0.485, 6.42], z ratio: 3.481, p_{FDR} =.001), while the difference between G0 and G1 (p_{FDR} >.1) was not significant. There was a quadruple interaction Generation * Perspective * Category * centered Age that was significant (p = .02) but not investigated further as it was not directly relevant to our main hypotheses and had a VIF > 20. Other interactions or main effects were non-significant (all ps > .059).

The same LMM was conducted excluding individuals with family links. The pattern of results was similar for the FMθ.

Correlations. We performed Pearson correlations on the amplitude of the LPP in each Perspective and the scores on the subscales of the PCL5. With the mean-to-mean approach, none of the correlations were significant after correcting for multiple comparisons for each perspective (all ps_{FDR} ≥.9). We performed the same analysis on G0 only and additionally performed correlations with the scores on the HTQ experience and total events. Again, none of the correlations were significant (all ps_{FDR} ≥.9). With the peak-to-peak approach, we observed a significant positive correlation between the LPP amplitude and the avoidance subscale when visualizing threatening images from the 1PP (r = .295, p_{FDR}<.001) and from the NoPP (r = .242, p_{FDR}=.035), with a higher LPP amplitude being associated with higher scores. Other correlations were not significant (all ps_{FDR}>.1). All correlations were not significant for the 3PP (all ps_{FDR} >.2). All the correlations conducted on G0 were not significant (all ps_{FDR} >.1).

For correlations with the FMθ, none of the correlations with the 1PP, 3PP and NoPP were significant (all ps_{FDR} >.7). The same correlations conducted on G0 with additionally the HTQ experience and total events, were also not significant for each perspective (all ps_{FDR} >.7).

3.3. SENSORY GATING

3.3.1. Auditory modality

We conducted LMM with Condition (Tone 1, Tone 2) as a within-subject factor, and PTSD (yes, no) and Generation (G0, G1, G2) as between-subject factors on the P50, N100, and P200, see Fig. 5**A**. Participants were included as a random grouping factor with a random intercept and a random slope for Condition. The fixed effects included Condition, PTSD, Generation, centered Age, and their interaction (ERP ~ Condition * Generation * centered Age * PTSD + (Condition | Participant)).

For the P50, we observed evidence of a significant main effect of Condition (χ^2=11.042, $p \le .001$), with a higher amplitude of the P50 for Tone 1 (mean: 0.39, CI_{95}:[0.14,0.65]) compared to Tone 2 (mean: −0.12, CI_{95}:[-0.38,0.14]; $mean_{diff}$ = 0.52, CI_{95}:[0.21, 0.82]). We also observed a triple interaction Condition*centered Age*PTSD (χ^2=11.312, $p \le .001$) and a quadruple interaction Condition*Generation*centered Age*PTSD (χ^2=6.824, p = .032). The same interaction without centered Age were not significant, suggesting that in this model, age explained more variance than Generation (all ps ≥ .3). All the other main effects or interactions were not significant (all ps ≥ .1). For the N100, we observed the same pattern of results, with a significant main effect of Condition (χ^2=61.579, $p \le .001$), with a higher amplitude of the N100 for Tone 1 (mean: −6.08, CI_{95}:[-6.58,-5.58]) compared to Tone 2 (mean: −4.30, CI_{95}:[-4.77,-3.82]; $mean_{diff}$ = −1.78, CI_{95}:[-2.23,-1.34]). We also observed a triple interaction Condition*Age centered*PTSD (χ^2=5.500, p = .019) a quadruple interaction Condition*Generation*Age centered*PTSD (χ^2=6.489, p = .038). The same interaction without centered Age were not significant, suggesting that in this model, age explained more variance than Generation (all ps ≥ .6). All the other main effects or interactions were not significant (all ps ≥ .058).

For the P200, we observed again a significant main effect of Condition (χ^2=201.930, $p \le .001$), with a higher amplitude of the P200 for Tone 1 (mean: 8.49, CI_{95}:[7.74, 9.24]) compared to Tone 2 (mean: 4.13, CI_{95}:[3.61,3.65]; $mean_{diff}$ = 4.36, CI_{95}:[3.76,4.96]). We also observed an effect of Condition*Generation (χ^2=8.947, p = .011), see Fig. 5**B**. Post-hoc comparisons indicated that all Generations had the classic sensory gating effect, with a reduced amplitude of the P200 for Tone 2 compared to Tone 1 (G0: $mean_{diff}$ = 3.10, CI_{95}:[1.72,4.48], z ratio:

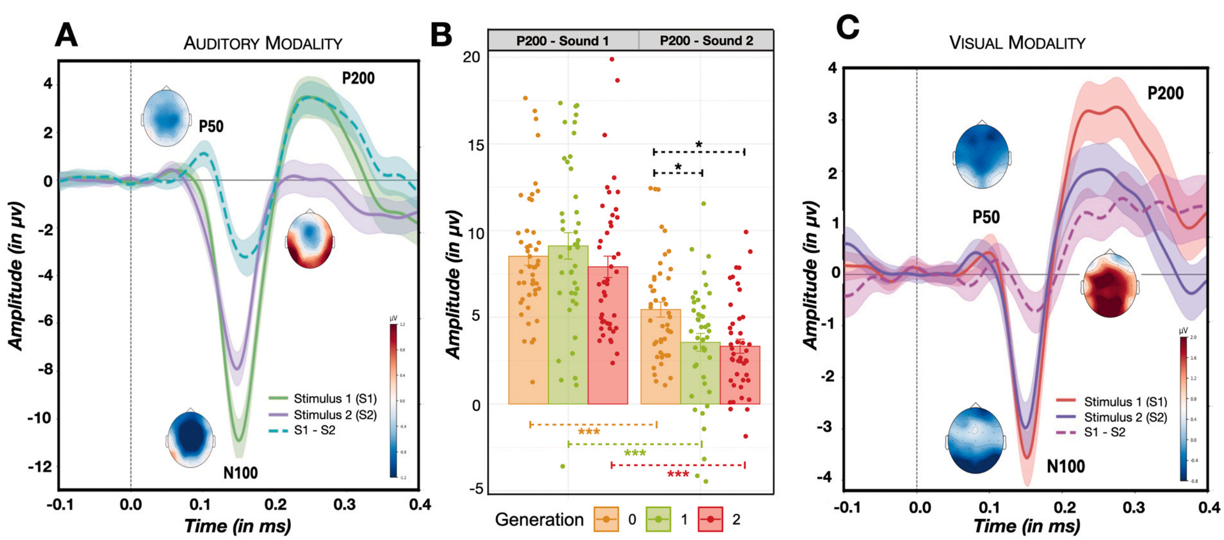

Fig. 5. A) Grand-averaged waves from all participants for the auditory modality at Cz, for Stimulus 1 (S1), S2, and their difference. B) Graphical representation of the P200 amplitude for S1 and S2 across Generation 0 (G0, in orange), Generation 1 (G1, in green), and Generation 2 (G2, in red). Colored dashed lines represent differences across conditions within a generation, while black dashed lines represent differences across generations within a single condition. All tests were two-tailed. * represents $p \ge .01$ and $\le .05$. * ** represents $p \le .001$. Error bars represent the Standard Error. C) Grand averaged waves from all participants for the visual modality on O1 and O2 for S1, S2 and the difference.

5.388, $p_{FDR} \leq .001$; G1: $mean_{diff} = 5.40$, CI_{95}:[4.17,6.63], z ratio: 10.470, $p_{FDR} \leq .001$; G2: $mean_{diff} = 4.58$, CI_{95}:[3.38,5.78], z ratio: 9.157, $p_{FDR} \leq .001$). When we compared Tone 1 and Tone 2 across generations, we observed that for Tone 1, none of the generations differed (all $ps_{FDR} \geq .3$). For Tone 2, the amplitude of the P200 was higher for G0 (mean: 5.33, CI_{95}:[4.35,6.30]) than for the other generations (G1: mean: 3.71, CI_{95}:[2.84,4.59], $mean_{diff} = 1.61$, CI_{95}:[-0.15,3.37], z ratio: 2.413, $p_{FDR} = .047$; G2: mean: 3.35, CI_{95}:[2.50,4.19], $mean_{diff} = 1.98$ CI_{95}:[0.24,3.71], z ratio: 3.009, $p_{FDR} = .015$). We also observed that Condition interacted significantly with centered Age (χ^2=7.927, $p = .004$), showing that age can also have an effect. Again, we observed that several interactions were significant when age centered was included, but not significant without centered Age (all $ps \geq .1$). All the other main effects or interactions were not significant (all $ps \geq .058$).

The same LMM was conducted excluding individuals with family links. The pattern of results was similar for the P50, N100 and P200.

Correlations. We performed Pearson correlations with FDR correction on the difference between S1 and S2 for the P50, N100 and P200, and the scores on the subscales of the PCL5. None of the correlations for the P50, N100, or P200 remained significant after correcting for multiple comparisons (all $ps_{FDR} \geq .1$). We performed the same analysis on G0 only and additionally performed correlations with the scores on the HTQ experience and total events. Again, none of the correlations were significant (all $ps_{FDR} \geq .4$).

3.3.2. Visual modality

The same linear mixed model (LMM) as for the auditory modality was conducted for the visual modality, see Fig. 5**C**. For the P50, only an interaction centered Age*PTSD was significant, but not investigated further as not relevant for our hypotheses. All the other main effects or interactions were not significant (all $ps \geq .1$). For the N100, we observed a main effect of Condition (χ^2=7.505, $p = .006$), with a higher amplitude of the N100 for Shape 1 (mean: −2.30, CI_{95}:-2.74,-1.86]) compared to Shape 2 (mean: −1.87, CI_{95}:[-2.26,-1.48]; $mean_{diff} = -0.429$, CI_{95}:[-0.74,-0.12]). We also observed an effect of Generation*PTSD (χ^2=6.351, $p = .041$), not investigated further as not relevant for our hypotheses. We also observed a triple interaction Condition*centered Age*PTSD (χ^2=4.112, $p = .42$), but the same interaction without centered Age where not significant ($p > .7$), suggesting that in this model, age explained a greater variance in the data than Generation. All the other main effects or interactions were not significant (all $ps \geq .1$). For the P200, we also observed a significant main effect of Condition (χ^2=47.124, $p \leq .001$), with a higher amplitude of the P200 for Shape 1 (mean: 4.77, CI_{95}:[4.2, 5.33]) compared to Shape 2 (mean: 3.31 CI_{95}:[2.9,3.73]; $mean_{diff} = 1.45$ CI_{95}:[1.04,1.86]). All the other main effects or interactions were not significant (all $ps \geq .1$).

The same LMM was conducted excluding individuals with family links. The pattern of results was similar for the P50 and P200. For the N100, we obtained a significant interaction Condition*PTSD (χ^2=4.200, $p = .040$) that was not significant with all participants included ($p > .1$). Post-hoc comparisons indicated that the difference between Shape 1 and Shape 2 was significant for individuals with PTSD ($mean_{diff} = -0.912$ CI_{95}:[-1.56,-0.26], z ratio: −3.588, $p_{FDR} = .001$), but not for individuals without PTSD ($p > .4$). The differences for individuals with PTSD compared to individuals without PTSD for Shape 1 or Shape 2 were not significant (all $ps > .5$).

Correlations. We performed exploratory Pearson correlations between the PCL-5 subscales (i.e., re-experiencing, avoidance, negative alterations, hyperarousal), the HTQ questionnaire (for G0 only), and the difference between S1 and S2 (i.e., S1 – S2) for the P50, N100 and P200 in the auditory modality. These correlations were performed based on either the peak-to-peak method or based on the mean-to-mean method. With the peak-to-peak approach, no correlations survived corrections for multiple comparisons in both modalities, also including the correlations conducted on G0 only (all $ps_{FDR} > .060$). With the mean-to-mean approach, none of the correlations for the P50, N100, or P200 remained significant after correcting for multiple comparisons in both modalities, also including the correlations conducted on G0 only (all $ps_{FDR} \geq .1$).

3.4. ODDBALL PARADIGM

We conducted LMM with Condition (standard, deviant) as a within-subject factor, and PTSD (yes, no) and Generation (G0, G1, G2) as between-subject factors on the P50, N100, and P200. To minimize the effect of Age that can account for possible effect of Generation, we centered Age per Generation and use it in our model as a covariate. We first tried with non-centered Age, but the multicollinearity with Generation was too high within each model. Participants were included as a random grouping factor with a random intercept and a random slope for Condition. The fixed effects included Condition, PTSD, Generation, centered Age, and their interaction (ERP ∼ Condition * Generation * centered Age * PTSD + (Condition | Participant)). For the MMN, as it requires a subtraction from deviant to standard tones which have an unequal number, it was not possible with the LMM and we performed a repeated-measures ANOVA.

For the P50, none of the main effects or interactions were significant (all $ps \geq .08$). For the N100, we observed evidence of a significant main effect of Condition (χ^2=58.474, $p \leq .001$), with a higher amplitude of the N100 for deviant tones (mean:-4.76, CI_{95}:[-5.16,-4.37]) compared to standard tones (mean: −3.70, CI_{95}:[-4.01,-3.40]; $mean_{diff} = 1.06$, CI_{95}:[0.79, 1.33]). We also observed a main effect of Generation (χ^2=7.161, $p = .027$) and an interaction Condition*Generation (χ^2=12.896, $p \leq .001$). We conducted post-hoc comparisons to evaluate the effect of Condition across each generation. We observed that for G0, the difference between standard tones and deviant tones was not significant ($p > .1$). For G1, we obtained the classic effect, with a higher N100 amplitude for deviant tones (mean: −4.86, CI_{95}:[-5.50,-4.23]) compared to standard tones (mean: −3.52, CI_{95}:[-4.01,-3.03]; $mean_{diff} = -1.343$, CI_{95}:[-1.87,-0.81], z ratio: −6.034, $p_{FDR} \leq .001$). We observed the same significant effect for G2, with a higher N100 amplitude for deviant tones (mean: −4.44, CI_{95}:[-5.15,-3.73]) compared to standard tones (mean: −2.95, CI_{95}:[-3.49,-2.40], $mean_{diff} = -1.491$, CI_{95}:[-2.20,-0.77], z ratio: −5.953, $p_{FDR} \leq .001$). We also compared the amplitude of the N100 for standard and deviant tones across generations. For deviant tones, none of the comparisons were significant (all $ps_{FDR} > .4$). For standard tones, G0 (mean:-4.64, CI_{95}:[-5.18,-4.10]) has a higher N100 amplitude than G1 (mean:-3.52, CI_{95}:[-4.01,-3.03]; $mean_{diff} = -1.120$, CI_{95}:[-2.18,-0.06], z ratio: −3.016, $p_{FDR} = .007$) and G2 (mean:-2.95, CI_{95}:[-3.49,-2.40]; $mean_{diff} = -1.694$, CI_{95}:[-2.81,-0.57], z ratio: −4.321, $p_{FDR} \leq .001$). G1 and G2 did not differ ($p_{FDR} > .2$). None of the other main effects or interactions were significant or relevant for our hypotheses ($p \geq .028$ & $\leq .905$). For the P200, the main effect of Generation and Age centered were significant but not investigated further as not relevant for our hypotheses. None of the other main effects or interactions were significant (all $ps \geq .09$). For the MMN, none of the main effects or interactions were significant (all $ps > .2$).

The same LMM was conducted excluding individuals with family links. The pattern of results was similar for the P50, N100, P200, and MMN.Fig. 6

Correlations. We performed exploratory Pearson correlations between the PCL-5 subscales (i.e., re-experiencing, avoidance, negative alterations, hyperarousal), the HTQ questionnaire (for G0 only) and the difference between standard tones and deviant tones (i.e., Deviant – Standard) for the P50, N100, P200 and MMN. These correlations were performed based on either the peak-to-peak method, or based on the mean-to-mean method. With the peak-to-peak method, when considering all generations together, for the P50, the N100 and the MMN none of the correlations reached conclusiveness in favor of H1 or significance after correction with the FDR approach (all $ps_{FDR} > .1$). For the P200, we observed evidence in favor of H1 for a positive correlation between the difference standard - deviant and the re-experiencing subscale (r = .298, $p_{FDR} < .001$). With the mean-to-mean approach, for the P50, the N100,

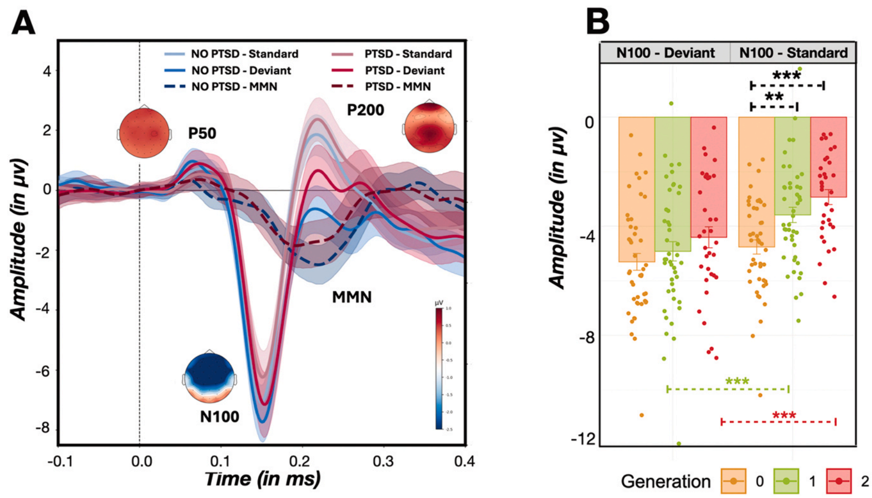

Fig. 6. A) Grand averaged waves on Pz, Cz and Fz from all participants for standard tones, deviant tones, and the MMN, for individuals with PTSD (red) and individuals without PTSD (blue). B) Graphical representation of the amplitude of the N100 for standard and deviant tones for G0 (orange), G1 (green) and G2 (red). All tests were two-tailed. * ** represents $p_{FDR} \leq .001$. * * represents $p_{FDR} \leq .01 \& > .001$. Error bars represent the Standard Error.

and the P200, none of the correlations were significant after FDR correction (all $ps_{FDR} > .1$). The same correlations conducted on G0 only with also HTQ were also not significant for the P50 (all $ps_{FDR} > .4$), N100 (all $ps_{FDR} > .2$) and P200 (all $ps_{FDR} > .6$).

4. Discussion

We offered a thoroughly transparent and well-powered study to understand whether non-affective and affective alterations persist several decades after a traumatic event, regardless of PTSD symptom presence, and whether such alterations are also observable in subsequent generations from the same society.

Even though the Cambodian genocide occurred about 50 years ago, we observed its long-lasting imprints as 32.75 % of the survivors recruited met the criteria for probable PTSD based on the Khmer version of the PCL-5 (Schaack et al., 2011). As noted in the method, it is important to acknowledge however, that a proper PTSD diagnosis was not clinically established in the present study due to the lack of access to Cambodian psychologists in rural regions. A previous study showed that between 8.5 % and 12.2 % of veterans met the criteria for PTSD diagnosis 40 years after the Vietnam War, based on the PCL-5 (Marmar et al., 2015). However, while their population had access to mental health services, none of our participants had such access, which can explain a higher prevalence of probable life-long PTSD. Critically, we observed a high prevalence of PTSD symptoms among both G1 and G2, with scores across the different subscales being statistically similar to those of G0. Such results may be related to a cumulative effect of different forms of trauma transmission and insufficient mental health support infrastructure, similar to a study conducted in rural Rwanda (Caspar et al., 2023). Furthermore, the specificities linked to the reconciliation process in Cambodia and the Extraordinary Chambers in the Courts of Cambodia (ECCC), which prosecuted fewer than 10 individuals for the genocide that decimated a quarter of the Cambodian population, may foster frequent feelings of revenge and anger in the population, potentially increasing or maintaining PTSD symptoms (Bockers et al., 2011).

To evaluate both affective and non-affective neural alterations, we used four tasks commonly reported in the trauma literature with EEG. We prioritized passive tasks to avoid the impact of unfamiliarity with technology on our results. Overall, we replicated several of the main task effects reported in the literature, demonstrating the reliability of our data despite the challenging testing conditions. However, some PTSD effects noted in the literature were not consistently observed and are discussed further in light of the time elapsed since the traumatic event and potential cultural differences.

In oddball tasks, the literature generally indicates that ERPs exhibit higher amplitudes for deviant tones than for standard tones (Tomé et al., 2015). This effect was observed here only for the N100, with a greater N100 amplitude for deviant compared to standard tones. In PTSD literature, the oddball task has been used to study alterations in arousal and reactivity in PTSD patients, with differences between standard and deviant tones. Previous studies using an auditory oddball task typically showed higher ERPs for deviant tones in individuals with PTSD compared to those without, indicating increased arousal for unexpected stimuli (Bangel et al., 2017; Felmingham et al., 2002; Ge et al., 2011; Lamprecht et al., 2004; Menning et al., 2008; Morgan & Grillon, 1999). In the present study, we did not find any effects of PTSD on early or late ERPs, but we observed an interaction of Condition with Generation on the N100. Results indicated that there was no difference between deviant and standard tones for G0, but such a difference was observed for G1 and G2. This finding rules out a potential cultural effect on the oddball effect, as G1 and G2 displayed the classic difference between deviant and standard tones. Additional comparisons revealed that while there were no generational differences for deviant tones, there was a significant difference for standard tones. Specifically, G0 exhibited a higher N100 amplitude for standard tones compared to G1 and G2. This result indicates that G0 does not attenuate responses to repetitive stimuli. In the literature, differences are typically observed for deviant tones (Bangel et al., 2017; Lamprecht et al., 2004; Menning et al., 2008). Here, our results suggest that the generation who survived the genocide does not exhibit enhanced processing of unexpected stimuli but instead shows a lack of attenuation in response to repetitive stimuli (Gjini et al., 2013; Neylan et al., 1999). One possible explanation is related to the specific characteristics of our sample, who survived a years-long genocide with constant threats, as opposed to other forms of trauma. This type of prolonged trauma may reduce the capacity to downregulate attentional resources, even for repetitive information. An alternative hypothesis is the impact of age, as previous studies have shown that the oddball effect on the N100 diminishes with age (Anderer et al., 1998; Friedman et al., 1993). In our analysis, we observed that age, when centered, interacted with the effect of condition, though to a lesser extent than generation. It could therefore partially account for the results as well.

Sensory gating tasks are used to study the filtering out of unnecessary or irrelevant sensory information. Consistent with the literature, we generally observed a higher amplitude of the ERPs (i.e., P50, N100, P200) on S1 compared to S2 in both modalities (Freedman et al., 1987), with the exception of the P50 in the visual modality. This result shows that our experimental paradigm was effective, despite being tested in a challenging context and with a population for which this paradigm had never been validated before. Prior studies have found that individuals with PTSD may have reduced sensory attenuation on S2, specifically on the P50, suggesting a difficulty in filtering out repetitive information (Gjini et al., 2013; Neylan et al., 1999). However, such results have not always been replicated in a sample composed of female veteran nurses (Metzger et al., 2002). In the present study, we did not observe an effect of PTSD in this task, consistent with Metzger and colleagues (2002), but our sample also included male participants. Particularly, in the auditory modality, for the P200, we observed a generational effect on the sensory gating effect. Comparisons revealed that while all generations displayed a classic sensory gating effect, G0 exhibited reduced attenuation (i.e., higher P200) for S2 compared to G1 and G2. This difference was not observed for S1, which is related to sensory encoding (Gjini et al., 2013). This finding suggests that G0 has difficulty filtering out repetitive information during the later stages of auditory processing. These results are somewhat consistent with those observed in the oddball task, as G0 had reduced attenuation of standard stimuli. Taken together, these findings may support the hypothesis that prolonged genocide-related trauma contributes to difficulties in downregulating processing, even for repetitive and non-threatening information. It has also been suggested that gender can influence sensory processing in PTSD populations and that the male-to-female ratio in study samples can impact observed effects (Karl et al., 2006). However, in this case, the VIFs in the model that included gender were too high to yield interpretable results.

In affective tasks on threat, the literature suggests that individuals with PTSD may exhibit an attentional bias towards threatening stimuli (Matsuo et al., 2003), along with an enhanced LPP to threatening or unpleasant images (Lobo et al., 2014; Macatee et al., 2021). However, this bias has also been associated with lower ERP amplitudes, indicating attentional disengagement from threat (Kounios et al., 1997; MacNamara et al., 2013). For the LPP, we observed that G0 exhibited a higher amplitude in the 1PP compared to the NoPP condition, suggesting enhanced processing of threats presented in the first perspective. Importantly, this effect was observed only in the human category and not in the animal category, indicating that heightened processing is specific to threats originating from humans. In contrast, G1 and G2 did not display any effects of perspective on the LPP amplitude in either the human or animal categories. This finding may be related to the fact that G0 endured trauma caused by other humans over many years, potentially leading to greater sensitivity to human-related threats. Additionally, G0 showed an overall higher LPP amplitude than G1 and G2 across both human and animal categories, suggesting a heightened sensitivity to threats in general. However, this effect was more pronounced when comparing G0 to G2 than to G1, which may indicate that sensitivity to threats diminishes across generations. Interestingly, we did not observe any interactions with PTSD, suggesting that this effect is more directly related to the experience of trauma itself rather than the development of PTSD. Regarding FMθ, previous studies have shown that it is higher when visualizing threatening stimuli compared to non-threatening ones (DeLaRosa et al., 2014). This aligns with literature linking FMθ to emotional or threatening stimuli (Aftanas et al., 2001, 2003), undesirable outcomes (Cohen et al., 2007), unpleasant experiences or events (Vecchiato et al., 2011), and negative affective states (Luu et al., 2000). However, a study comparing PTSD to non-PTSD individuals found reduced EEG power in this band during threatening combat scenes in PTSD patients compared to a control group (DeLaRosa et al., 2020). The authors interpreted this as indicating reduced regulation of affective memories in PTSD patients. In our study, however, G0—who directly experienced genocide-related trauma—exhibited higher FMθ in 1PP compared to NoPP in the human category and overall greater FMθ compared to other generations. This may indicate greater threat sensitivity in G0 (Aftanas et al., 2003). For G1 and G2, this difference was present only in the animal category and not in the human category. Importantly, we again found no effect of PTSD, but rather an effect of generation. This suggests that the results are driven by the experience of a traumatic event itself rather than differences in PTSD scores. Due to the lack of previous cross-cultural literature, it is challenging to identify a single factor accounting for the differences between our study and that of DeLaRosa and colleagues. Several variables differ, such as time since trauma, cultural background, and age. Additionally, DeLaRosa and colleagues used FPz as the reference electrode, which is uncommon in this literature (Cohen & Cavanagh, 2011). Future studies should address these differences to better understand the observed discrepancies. A general limitation of our study, as well as that of DeLaRosa and colleagues, is that the NoPP condition included images depicting non-threatening scenarios from various perspectives, including 1PP (first-person perspective) and 3PP (third-person perspective). To ensure more stable effects, future studies should consider standardizing the no-threat condition to a single perspective.

Previous studies indicated that individuals with PTSD (Miller et al., 2021; Passardi et al., 2018, 2019; Poljac et al., 2011) and the next generation (Castro-Vale et al., 2020b) might have impairments in recognizing emotions. However, our study failed to replicate these findings, as we observed no effect of PTSD on emotion recognition. Instead, we found a main effect of Generation for correct responses, reaction times, and P3 amplitude, which did not interact with other factors. Overall, G0 had fewer correct responses, slower reaction times, and a higher P3 amplitude compared to G1 and G2. One interpretation, based on trauma literature, is that G0's emotion recognition abilities are impaired, leading to worse and slower performance compared to the other generations, but they may process more of the emotions displayed. However, this could also be attributed to age, as it is well-established that elderly individuals tend to perform more poorly and slowly in such tasks (Ruffman et al., 2008). We also observed a main effect of Condition, with higher correct responses for happy faces compared to neutral and sad faces. However, this may be due to an experimental confound, as the individuals on the pictures were smiling with an open mouth for happiness, but with a closed mouth for sad and neutral faces (Bouvier et al., 2008). We further observed that certain miscategorizations correlated with hyperarousal and negative alteration subscales, suggesting that a more pronounced symptomatology is associated with more errors. One possible interpretation is that the longer time distance between the traumatic experience and the testing might reduce alterations in emotion recognition over time. An alternative interpretation is culture-related. The influence of living in a collectivist or individualist society on emotion recognition is indeed a current topic of debate (Keshtiari & Kuhlmann, 2016; Mishra et al., 2018; Prado et al., 2014). Our participants, living in Southeast Asia, were from a collectivist culture according to the literature (Oyserman et al., 2002). Based on this hypothesis, living in such culture and in large groups might prevent alterations in emotion recognition after trauma. However, the majority of the literature on alterations in emotion recognition is western-centered, and further experimental studies in collectivist cultures are needed to confirm this postulate.

The study faced several limitations inherent to the population we tested and field research. Firstly, numerous participants from Generation 0 (G0) reported experiencing brain injuries, suffocation, and loss of consciousness at some point in their lives, but many were unable to recall specific dates or determine if these incidents occurred before, during, or after the Khmer Rouge regime. This uncertainty makes it difficult to assess the impact of such traumas on our findings. We also did not find an adapted Khmer version of a questionnaire to assess these events in G1 and G2 that was specifically tailored to the Cambodian population, thus lacking this information in our sample. Another challenge was the inability to recruit three generations from the same family due to various field constraints, which impeded our third scientific aim in the present paper and resulted in a cross-generational study. This limitation means our conclusions are about the general effects of trauma across generations within a specific society, without considering potential genetic factors. Some of our participants had family links, but not enough to conduct reliable statistical analyses. The same analyses conducted without the few individuals with a family link in our sample showed overall similar effects across tasks. Nonetheless, we observed small differences in the emotion recognition task for the P300 and in the threat processing task for the LPP. However, due to the limited number of individuals with a family link, it is not possible to reliably interpret these results, which may merely reflect individual effects. Future cross-generational studies could compare individuals with and without genetic links to explore the roles of shared environmental and/or genetic factors in the intergenerational transmission of trauma in a given society. Also, integrating a control group that had not experienced the Cambodian genocide would have led to stronger conclusions regarding its impact. However, since the Khmer Rouge regime lasted for about four years and affected the entire country, we were unable to find individuals who had not been exposed to these events, despite recruiting participants from various regions. Lastly, the complexity of recruiting and testing our target population in Cambodia, using unfamiliar equipment, posed significant challenges and resulted in some data loss.

While we broadly replicated effects reported in the literature for the tasks we used, we also observed evidence for opposite effects or no evidence for an effect in some cases. One possible interpretation for these discrepancies is cultural differences, but they may also be associated with our statistical approach and data analysis methods. Indeed, while most studies in the literature rely on ANOVAs and mean averaging, linear mixed models incorporate single-trial extractions and the inclusion of random effects (i.e., random intercepts and slopes; (Barr, 2013; Heise et al., 2022; Hu et al., 2011; Mir et al., 2014)). Furthermore, the method used to extract ERPs could contribute to these differences. A notable observation in our study was that we obtained more significant correlations when using the peak amplitude approach for extracting ERPs compared to the mean amplitude approach. Previous literature on PTSD similarly indicates that more correlations emerge with the peak amplitude method (Araki et al., 2005; Felmingham et al., 2002; Gillette et al., 1997; Gjini et al., 2013; Menning et al., 2008) than with the mean amplitude approach (Bangel et al., 2017; Ge et al., 2011). However, it has been suggested that peak amplitude can be biased by noise, potentially leading to an overestimation of the true amplitude value (Clayson et al., 2013; Heise et al., 2022; Luck, 2005). This highlights the importance of using methods more robust to noise (i.e., mean amplitude) that could better take into account intra-subject variability (i.e., linear mixed models). These methodological issues should be more thoroughly discussed in the existing trauma literature as they may also account for differences.

To summarize and conclude, the present study was structured around three main research questions, which focused on the relationship between PTSD and physiological reactivity in a cross-generational sample of people who lived through a major cultural trauma. Regarding the presence of (non-)affective neural alterations five decades after a trauma, we observed significant effects of generation on threat processing in the LPP, with sensitivity to threat being higher in G0 than in subsequent generations. This result suggests that sensitivity to threat can last for a very long period and may be associated with personal threatening experiences, while other alterations may not be as persistent. We also observed that G0 did not display classic attenuation over S2 in the auditory sensory gating task for the P200, and showed reduced attenuation over standard tones for the N100 in the oddball task. This result also supports the notion that some alterations, particularly in the attenuation of repetitive stimuli, may persist even five decades after a trauma. Importantly, several effect of PTSD reported in the literature (Karl et al., 2006; Miller et al., 2021) were not found in the present study, with mostly an effect of Generation. A possible interpretation is that most neural alterations linked to specific PTSD scores may be reduced decades after a trauma, as our sample experienced a huge traumatic event half a century ago, a time gap larger than in most previous studies. It would be relevant to understand when neural alterations tend to be reduced, and if access to mental health facilities can reduce this time. However, it is also worth noting that a fair majority of previous studies in the PTSD literature suffer from insufficient sample sizes or non-adapted control samples (Miller et al., 2021), which could have lead to less reliable findings. The correlations we observed with the peak-to-peak approach between PTSD symptomatology and neural alterations are consistent with the literature, and interestingly, such correlations were never found with the number of traumatic experiences as measured with the Harvard Trauma Questionnaire. This may suggest that these alterations are a general consequence of trauma rather than depending on its quantity. Following our research question regarding the cross-generational transmission of (non-)affective neural alterations, we observed in all tasks that G1 and G2 did not appear to display such alterations despite similarly high scores on the PTSD scale as G0. This result suggests a dissociation between the neural alterations and the reported PTSD symptoms. Finally, and following our third objective, we aimed to go beyond the classic WEIRD centrism in the literature. Interestingly, we found all the classic task effects reported in the literature, suggesting that such processes could be universal, but the critical lack of studies on non-WEIRD populations prevents us from reaching stronger conclusions on this aspect. However, taken as a whole, the present study also serves as proof that evaluating the impact of cultural trauma on underrepresented groups, even with electrophysiological tools, is largely possible. Psychology and neuroscience are currently at a crossroads, where the robustness of their findings is increasingly questioned due to the narrow demographics of their study samples, in addition to other practices (e.g., statistics, transparency) (Arnett, 2016; Caspar, 2024). We hope that this study will open the path to more neuroscience-based research on PTSD and trauma across various populations.

Role of Funding

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Declaration of Generative AI and AI-assisted technologies in the writing process

The authors used ChatGPT (OpenAI) to check for the presence of typos or possible grammatical mistakes in the manuscript, none of the authors being native English speakers. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

Author contribution

E.A.C. developed the study concept. E.A.C. and G.P.P created the study design. G.P.P. created the experimental scripts. P.R. provided support in Cambodia and help to recruit participants. E.A.C. and G.P.P. conducted the study and analyzed the results. E.A.C. wrote the first draft and G.P.P. and P.R. provided comments. All authors approved the final version of the manuscript.

CRediT authorship contribution statement

Caspar Emilie: Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Pech Guillaume P.:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Ros Pheak:** Writing – review & editing, Validation, Supervision, Resources, Project administration.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2025.109028.

Data availability

Link is in the manuscript

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